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The red turpentine beetle, *Dendroctonus valens* LeConte (Scolytidae): an exotic invasive pest of pine in China

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Abstract. An exotic invasive pest of pines, the red turpentine beetle, *Dendroctonus valens* LeConte (Scolytidae) (RTB), was first detected in Shanxi Province, northern China, in 1998 and started causing widespread tree mortality there in 1999. This outbreak continues and has spread to three adjacent provinces, causing unprecedented tree mortality. Although it is considered a minor pest of pines in North America, RTB has proven to be an aggressive and destructive pest of *Pinus tabuliformis*, China's most widely planted pine species. The bionomics and occurrence, distribution, response to host volatiles, and host preference of this pine beetle in China are compared with what is known of the beetle in its native range in North America. Factors likely contributing to *D. valens* success in China and control of the beetle outbreak are discussed. (−)-β-pinene was shown to be the most attractive host volatile for *D. valens* from the Sierra Nevada of California, whereas 3-(+)-carene is the most attractive host volatile for beetles in China. Monocultures of *Pinus tabuliformis*, several consecutive years of drought conditions and warm winters have apparently factored *D. valens* invasion and establishment in China.

Introduction

The red turpentine beetle, *Dendroctonus valens* LeConte (Coleoptera: Scolytidae), is a common pest of pines in its native range in North and Central America (Eaton and Lara 1967). It is considered to be a secondary pest and is often associated with more aggressive bark beetle species. Tree mortality and outbreaks attributed to *D. valens* alone are rare in its native range (Smith 1971; Cibrian et al. 1995). Recently, it has been reported as the cause of ponderosa pine (*Pinus ponderosa* Lawson) mortality in plantations in California and Mexico (Rappaport et al. 2001).

Dendroctonus valens was introduced into China in the early 1980s when unprocessed logs were imported from the west coast of the United States (report on file at Chinese Academy of Sciences, Beijing). A report of plant diseases and insect pests in Shanxi province in the early 1980s provides no record of *D. valens* activity (Ying and Huang 1984). During those years, Shanxi province imported large quantities of unprocessed ponderosa pine logs for coal mine timber. *D. valens* was first discovered in *Pinus tabuliformis* forests in Qinshui and Yangcheng, Shanxi province, in 1998 and its first outbreak occurred in 1999 in many regions of Shanxi. DNA analysis indicates that western North America is the source of China's *D. valens* (personal communication with Anthony Congeto, Texas A & M University). Since 1999, *D. valens* has spread rapidly from Shanxi province to the adjacent provinces of Hebei, Henan, and Shaanxi and infested over 500,000 ha of pine forest, causing extensive tree mortality. More than 10 million *Pinus tabuliformis* Carr. have been killed, as well as other pine species, including *Pinus bungeana* Zucc (Li et al. 2001; Miao et al. 2001; Zhang et al. 2002). Several consecutive years of drought conditions have stressed *P. tabuliformis* stands and contributed to the outbreak (Li et al. 2001). Because pines are a major reforestation species in China and *P. tabuliformis* widely planted across a large portion of the country, the potential range of *D. valens* is nationwide (Britton and Sun 2002). Herein is an evaluation of factors that likely have contributed to the current outbreak of *D. valens* in China and may influence its future course.

Bionomics and occurrence

The life circle and behavior of *D. valens* appear similar in North America and the People's Republic of China (Table 1). However, some notable differences exist. Foremost among these is the beetle's ability to colonize, kill, and reproduce in mature *P. tabuliformis*, resulting in an outbreak that has no parallel in the native range of *D. valens*. In North America, *D. valens* is reported to initiate attack on the tree near ground level and colonize a short distance both upward along the lower bole and downward along the upper roots (Smith 1971). In China, *D. valens* extensively colonizes and overwinters in roots (Britton and Sun 2002; Wu et al. 2002). It is speculated that extensive root colonization, in combination with the inoculation of fungal associates into roots, may help explain the beetle‘ tree-killing success in China (Owen 2001). In the United States, fungi isolated from *D. valens* include *Leptographium terebrantis, L. procerum, Ophiostoma ips*, and a *Graphium* spp. (Owen et al. 1987; Klepzig et al. 1991). Among the *Ophiostoma* fungi carried by *Dendroctonus* bark beetles attacking ponderosa pine, *L. terebrantis* proved the most virulent (Owen et al. 1987 Parmeter et al. 1989). *L. terebrantis* has also been associated with the decline and mortality of a number of other *Pinus* spp. (Highley and Tattar 1985; Klepzig et al. 1991; Bannwart et al. 1998). It is yet unknown which, if any, of the know fungal associates of RTB are present in China or if RTB has formed new associations since its introduction.

The flight distance of *D. valens* in the United States of America can exceed 16 km (Smith 1971). In China, flight distances up to 35 km have been documented (Zhang et al. 2002). In China, no life stages of *D. valens* can overwinter in boles when the temperature is below −18 °C (Wu et al. 2002). Little

Table 1. Comparison of bionomics and occurrence of *D. valens* in northern People's Republic of China and western North America.

	Western North America[a]		China[b]	
Longitude	60W to 97W and 103W to 125W[c]		110E to 115E	
Latitude	15°N to 55°N (mainly 30°N to 50°N)[c]		35°12′N to 39°16′N	
Host	All *Pinus* species including:		*Pinus* species including:	
	Pinus ponderosa[d]	*Pinus lambertiana*	*Pinus tabuliformis*[e]	
	Pinus strobes	*Pinus resinosa*	*Pinus bungeana*	
	Pinus rigida	*Pinus contorta*	*Pinus aramandii*	
	Pinus echinata	*Pinus banksian*		
	Pinus radiate			
Occasional Hosts	*Picea*, *Pseudotsuga*, *Larix*, *Abries*		*Picea meyeri*	
Life stages	Egg	2 week	Egg	1–2 week
	Larvae	8 week	Larvae	8–10 week
	Pupae	1 week	Pupae	1–2 week
	Young adult	1 week	Young adult	1 week
Flight temperature	19–23 °C		14–28 °C	
	Peak flight and attack activity usually occur in spring. In the warmer parts of its range (southern areas), RTB may occur during intermittent warm periods in the winter; In the colder parts, the winter is passed in hibernation, chiefly in the adult stage and to a lesser extent in larval stage.		Flight of overwintered adults begins in Mid April and peaks in mid May. Pupation of overwintered larva begins in early June, and eclosion begins in early July. *D. valens* adults can be detected from May to October.	
Flight distance	More than 16 km (more than 10 miles)		Generally 20 km, Farthest flight distance is 35 km	
Attack pattern	Bases of trees, concentrated in the basal 1.8 meter of the tree, colonize a short distance both up and down to the upper roots and lower bole		Bases of the tree, roots extensively colonized and serve as overwintering sites	
Aggressive behavior	Freshly cut stumps, the bases of trees that are dying, diseased or attacked by other insects; exposed roots and the bases of trees that are weakened or injured. Fire-scorched trees and trees in campgrounds and around homes also are frequently attacked		Similar to those of the population in the western North America. When the population density is high and the canopy density of stands is low, the pest can quickly attack healthy trees with a breast-height diameter greater than 10 cm and over 20 years old	

[a] Cited from Smith (1971), Gara and Vité (1962), Vité et al. (1964).

[b] Cited from Miao et al. (2001), Zhang et al. (2002), Wang et al. (2002), Wu et al. (2002).

[c] North American distribution from Smith (1971).

[d] Pine species that is most frequently attacked (Smith 1971).

[e] Pine species most frequently killed in China.

mortality occurs among larvae and adults that overwinter in the roots (Miao et al. 2001), however, indicating that roots are important for *D. valens* survival in China (Wu et al. 2002). *D. valens* primarily attacks *Pinus tabuliformis* Carr. and *Pinus bungeana* Zucc, especially the former, in China. It has been reported from *Pinus armandi* Franch, and *Picea meyeri* Redh. et Wils, but damage on these hosts is not confirmed (Zhang et al. 2002). As a major reforestation species in China, *P. tabuliformis* is widely planted across a large portion of the country, including degraded and marginal sites that contribute to tree stress and likely favor *D. valens* activity (Li et al. 2001). In general, mature and overmature *P. tabuliformis* forests are infested, while younger forests are seldom attacked (Miao et al. 2001). In *D. valens*-infested pine forests are also endangered by another beetle, *Hylastes parallelus* Chapuis (Wu et al. 2002). The interaction between these two beetles and the role of *H. parallelus* in *D. valens* infestation are unknown.

Predators of *D. valens* in China are rare although *Dendrocopos major* Linnaeus (Piciformes: Picidae), *Labidura riparia* (Dermaptera: Labiduridae), *Raphidia sinica* Steinmann (Neuroptera: Raphidiidae), *Tetramorium guineense* Fabricius (Myrmicinae: Tetramoriini), two species of Paederus Fabricius (Coleoptera: Staphylinidae), one species of Thanasimus Latreille (Coleoptera: Cleridae), one species of Cryptolestes Ganglbauer (Coleoptera: Ostomatidae), one species of Hister L. (Coleoptera: Histeridae) and one species of Colydiidae (Coleoptera) have been found in limited numbers (Zhang et al. 2002). A adult of Tenebrionidae species (Coleoptera) proved to be a highly effective predator of *D. valens* adults in the laboratory (Wu et al. 2002). Identified pathogens of *D. valens* larvae, pupae and adults in China include two fungi of Monilianes, Hyphomycetis: *Beauveyia Vuillemin* and *Metarrhizium anisopliae*, which killed larvae, adult, and pupae of *D. valens* (Wu et al. 2002; Zhang et al. 2002).

Distribution

Except for the southern Atlantic Coast and Gulf Coast States, *D. valens* is common in pine and mixed conifer forests of the northeastern and western United States, southern Canada, Mexico, and Honduras (Bright 1976; Figure 1). Its native range extends roughly from 15°00′N to 60°00′N latitude, but it is concentrated between 30°00′N to 50°00′N (Wood 1963, 1982; Bright 1976). In China, *D. valens* is widely distributed in Shanxi province, and parts of the adjacent provinces of Hebei, Henan, and Shaanxi (Figures 1 and 2). The most heavily attacked forests are located in the Taihang, Lulang, and Zhongtiao Mountains in Shanxi province 35°12′N to 39°16′N latitude, from 600 to 2000 m elevation (Zhang et al. 2002). The latitudinal range of *D. valens* in North America corresponds well with the latitudinal range of China's national boundaries and native pines therein. There are expensive pine forests in the mountains of China are less than 3000 m in elevation and so the potential range of *D. valens* is much wider than its current distribution (Song et al. 2000; Figure 2).

D. valens has spread rapidly in China since its first outbreak in China in 1999 (Li et al. 2001; Miao et al. 2001). To date, it has been found in 62 counties, eight forestry Bureaus and two afforested mine stands in four provinces

Figure 1. Distribution of *D. valens* in northern China: including Shanxi, Hebei, Henan, and Shaanxi provinces. Insert shows *D. valens* distribution in North America (Smith 1971; Pajares and Lanier 1990).

(Shanxi, Shaanxi, Hebei, and Henan), and infested over half a million ha of pine stands.

Geographical variations of *D. valens* response to host volatiles

D. valens is known to attack diseased or wounded pines (Eaton and Rodriguez Lara 1967), relying on host odors or kairomones to locate and select its host. *D. valens* is attracted to the resin odors of its host ponderosa pine, *Pinus ponderosa* Lawson (Vité and Gara 1962; Vité et. al. 1964; Owen 1985; Hobson 1992). The principal monoterpene components that attract *D. valens* to ponderosa pine in California are (−)-β-pinene, 3-carene and (+)-α-pinene (Hobson et al. 1993; White and Hobson 1993; Hobson 1995). (−) and (+)-α-Pinene are different in their attractiveness, and (−)-α-pinene alone did not attract *D. valens*. Adding the (−)-enantiomer interrupted attraction to (+)-α-pinene (Hobson et al. 1993), (−)-β-pinene was the most attractive component (Hobson et al. 1993) and elicited the greatest antennal response. In addition, a different response was observed to (−) and (+) α-pinene and (−) and (+)-limonene (White and Hobson 1993). The response of *D. valens* to host semiochemicals in China was distinctly different from that reported in the

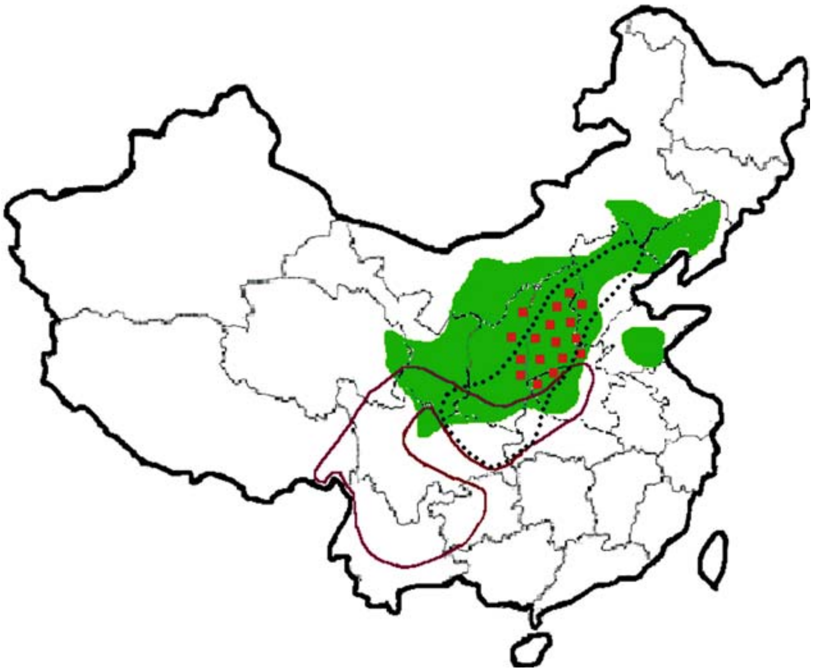

Figure 2. Species distribution map showing (distribution of *D. valens*, dots): *P. tabuliformis* (shaded), *P. bungeana* (dashed line) and *P. armandi* (solid line) in China.

above studies, which used beetles from the central Sierra Nevada. In the Chinese population, (+)-3-carene was the most attractive host monoterpene tested (Guo et al. 2003; Sun Jianghua et al. in press). It attracted significantly more beetles than any other single monoterpene [(+)-α or (−)-β-pinene] or any of the ternary or quaternary blends tested, including the standard *D. valens* lure used in North America [a 1:1:1 blend of (+)-α-pinene, (−)-β-pinene, and (+)-3-carene]. (−)-β-Pinene and (+)-α-pinene, presented individually, were not significantly more attractive than control tests. Adding limonene to the standard lure significantly decreased beetle response. These results illustrate regional variation in *D. valens* response to host volatiles (Guo et al. 2003; Sun Jianghua et al. in press) and may provide clues to the origin of *D. valens* in China. Recognition of this variation in beetle response enables us to formulate more effective lures for trapping and monitoring *D. valens*.

Pheromones produced by *Dendroctonus brevicomis* Leconte and *Ips* spp. may be weakly attractive to *D. valens* or increase *D. valens* response to host volatiles Raffa 1991; Paine and Hanlon 1991; Erbilgin and Raffa 2000). 4-Allylanisole [1-methoxy-4-(2-propenyl) benzene] is present in oleoresin of various pine species (Drew and Pylant 1966; Werner 1972; Pierce et al. 1987; Hayes et al. 1994) and is an attractant to *D. valens* when released at a low rate, but not at a high rate (Gladwin et al. 2001). Ethanol also occurs naturally in trees and is an important host-derived semiochemical. It is a product of fermentative respiration in plant tissues and is usually associated with hypoxic or anoxic conditions (Davies 1980; Bennett and Freeling 1987; Harry and Kimmerer 1991). Ethanol, released alone or in combination with host terpenes, is a well-known primary attractant for various species of scolytid secondary bark beetles (Moeck 1970; Klimetzek et al. 1986; Nordlander et al. 1986; Phlips et al. 1988; Chénier and Philogène 1989; Liu and McLean 1989; Schroeder and Lindelöw 1989; Sjödin et al. 1989; Byers 1992; Kelsey 1994a, b). *D. valens* was attracted to ethanol released in combination with a mixture of α-pinene and (β-pinene (1:1). It responded about four times more frequently to traps with a high ethanol release rate, compared to a low rate, regardless of 4-allylanisole levels, in Central Oregon (Gladwin et al. 2001). Traps baited with a 1:1 ethanol-turpentine mixture captured 60 times more *D. valens* than traps with turpentine alone in Wisconsin (Klepzig et al. 1991). The other test in Wisconsin indicated that attraction varied with trap type and ratio of ethanol:α-pinene. Lower stem flight traps captured nearly five times as many *D. valens* as did pitfall traps, suggesting that trap design is important for monitoring and managing *D. valens*. All combinations of α-pinene plus ethanol, with the exceptions of 5:1 ratio of ethanol: (+)-α-pinene and 1:1 ratio of ethanol:(−)-α-pinene, attracted more *D. valens* than did unbaked controls. *D. valens* did not show any overall preference between the enantiomers of α-pinene or between the ratios (Erbilgin et al. 2001), but the numbers responding were very low overall. Oleoresin in healthy trees usually contains higher concentrations of 4-allylanisole than stressed trees (Cobb et al. 1972; Nebeker et al. 1995), and 4-allylanisole levels are therefore presumed to serve as a kairomone for beetles in search, of hosts with reduced defenses. Lower quantities of 4-allylanisole in stressed and diseased pines could be partially responsible for their greater vulnerability to bark beetle attacks than healthy trees (Stark et al. 1968). In contrast to 4-allylanisole, which increases in healthy trees, ethanol accumulates in severely stressed, dying, or recently dead trees. High ethanol concentrations have been reported in tissues of flooded (Joseph and Kelsey 1997), mechanically injured (Sjödin et al. 1989), and diseased trees (Kelsey et al. 1998), stumps (Kelsey and Joseph. 1999a) and logs (Kelsey and Joseph. 1999b). These findings are consistent with the observation that *D. valens* prefers weakened, injured or stressed trees to healthy ones.

The beetle-produced (−)-verbenone (4,6,6-trimethylbicyclo[3.1.1.]hept-3en-2-one) was shown to be an inhibitor of *D. valens* response to host volatiles. In studies conducted in California, the release of pure verbenone from bubblecaps or a microencapsulated (MEC) formulation reduced the response of *D. valens* to a mixture of three host volatiles, (+)-α-pinene. (+)-Δ-3-carene, and (−)-β-pinene (1:1:1) by 82.1 and 89.3%, respectively (Rappaport et al. 2001). Two release systems of verbenone were tested for protection of *P. tabuliformis* from attack in China: (1) polyethylene bubblecaps (BC) filled with 800 mg of neat verbenone and (2) a sprayable water suspension of microencapsulated (MEC) verbenone. Treatments included both live trees

Table 2. Response of *D. valens* to semiochemicals.

	California[a] US	Wisconsin[b] US	Oregon[c] US	Shanxi[d] China
(−)-β-Pinene	Attractive			Non-attractive
(+)–3-Carene	Attractive	Attractive		Attractive
Myrcene	Attractive			
(−)-Limonene	Non-attractive			
(+)-Limonene	Non-attractive			
(−)-α-Pinene	Non-attractive	Attractive		
(+)-α-Pinene	Attractive	Attractive		Non-attractive
Ethanol			Attractive	
Verbenone	Disruption			Disruption
(+)-α-Pinene plus ipsenol		Attractive		
(−)-α-Pinene plus ipsenol		Attractive		
(−)-α-Pinene plus ethanol		Attractive		
(+)-α-Pinene plus ethano1		Attractive		
Mixture of (+)-α-Pinene, ipsdienol and lanierone		Attractive		
Mixture of (−)-α-Pinene, ipsdienol and lanierone		Attractive		
Mixture of (−)-β-Pinene, ipsdienol and lanierone		Attractive		
Mixture of (+)–3-Carene, ipsdienol and lanierone		Attractive		Attractive
Mixture of (−)-α-Pinene, (−)-β-Pinene and (+)–3-Carene				Attractive

[a] Hobson et al. (1993); Rappaport et al. (2001).
[b] Erbilgin and Raffa (2000), Erbilgin et al. (2001).
[c] Gladwin et al. (2001).
[d] Guo et al. (2003), Sun et al. (2003).

and surrogate trees (cardboard cylinders coupled with Lindgren pheromone traps) baited with host volatiles. Both release systems significantly reduced trap catch for real trees and surrogate trees, and there was no difference in effectiveness between the verbenone treatments. Equal numbers of male and female beetles responded to all treatments, suggesting that none of the semiochemical formulations had a sex-specific effect. When applied to real trees, both release systems provided significant protection, reducing numbers of beetle attacks per tree from a mean of 5.1 to a mean of 0.7 (for both release systems) (Sun et al. 2003). Responses of *D. valens* to some semiochemicals are summarized in Table 2.

Host preference

In North America, *D. valens* attacks all species of pine within its range and occasionally spruce and larch (Bright 1976; Furniss and Carolin 1977; Cibrian et al. 1995). In the Western United States, *Pinus ponderosa*, *P. contorta*,

Table 3. Resin volatiles found in various *D. valens* hosts.

Pine species	Percent of total resin volatiles of pine species								
	Pp[a,j]	Pr[b,j]	Pa[c,k]	Pm[d,k]	Pt[e]	Pt[f]	Pt[g,l]	Pm[h,l]	Pa[i,l]
S-(−)-β-Pinene	35.8	43.86	15.5	8.9	1.8	13	0.7	1.2	2.3
S-(+)—Carene	34.4	Trace	0.4			12			1.4
Myrcene	7.0	Trace	0.7	1.4	0.5		0.4	0.4	0.6
S-(−)-Limonene	5.5								
		2. 57[m]			0.8[m]	13[m]			
R-(+)-Limonene	< 0.1								
S-(−)-α-Pinene	14.3								
		12.43[m]	80.7[m]	86.2[m]	91.8[m]	< 2[m]	39.4[m]	31.7[m]	21.8[m]
R-(+)-α-Pinene	0.9								
S-(−)-β-phellandrene	0.6	–	0.8[m]	1.5[m]	0.1[m]		0.1[m]		
α-Turpinene						> 50	0.6	Trace	0.1
α-Turpineol					0.2		0.1		
Ocimene						6			
α-Cedrene					0.2		0.1	0.6	Trace
Longifolene					1.5		0.7	9.5	1.7
Caryophyllene					0.3		Trace	1.4	
Camphene			0.4	0.9	1.0		0.4	0.5	0.3
Dipentene			0.9	1.0			0.7	0.5	0.8

[a] *Pinus ponderosa.*

[b] *Pinus radiate.*

[c] *Pinus armandii.*

[d] *Pinus massoninan.*

[e] *Pinus tabuliformis*, from steam distilled gum turpentine *of Pinus tabuliformis*, from Taiyuan district, Shanxi province (Weissmann and Lange 1988).

[f] *Pinus tabuliformis*, emitted from *Pinus tabuliformis* twigs and leaves of Beijing, the terpene emission rate increases with irradiation and temperature and the rate has two park values during noon and middle night (minor) except for α-pinene and ocinene (Li et al. 1994).

[g] *Pinus tabuliformis.*

[h] *Pinus massoninan.*

[i] *Pinus armandii.*

[j] From White and Hobson (1993).

[k] From steam distilled gum turpentine of *Pinus massoninan* from Hongjiang, Hunan province and of *Pinus armandii* from Guiyang, Guizhou province (Su et al. 1981).

[l] From oleoresin of boles of *Pinus* species from Zhongtiaoshan Mountain, Shanxi province (Song et al. 1993).

[m] The proportion of (+) and (–) enantiomer of the components was not given.

P. Jeffreyi, *P. lambertiana*, *P. monticola*, and *P. radiata* are preferred hosts, with Monterey pine (*P. radiata* reported as the tree most frequently killed and ponderosa pine (*P. ponderosa* is the tree most frequently attacked (Smith 1971). In China, its primary host is *P. tabuliformis* (Li et al. 2001; Miao et al. 2001). Occasionally it may be found on *P. armandi* Franch and *Picea meyeri* Redh. et Wils, but damage on these hosts is not confirmed (Zhang et al. 2002; Table 1), *Pinus sylvestnis* var. *mongolica* Litv, a rare species in Shanxi province of China, has occasionally been attacked by *D. valens*. Evidence suggests that *D. valens* will attack all Asian pine species as it continues to spread. The components of resin volatiles of many Chinese *Pinus* species are given in Table 3. α-Pinene and β-pinene consistently rank as primary components of volatiles from Chinese species and species from the western United States. The percentage of 3-carene, the most effective attractant to Chinese *D. valens*, largely varies with collection site.

Factors related to *D. valens* success in China

Stages that are necessary for successful introduction and subsequent invasion include (a) introduction of a species into a new habitat, (b) initial colonization and successful establishment of a species, and subsequent dispersal and secondary spread into new habitats (Sakai et al. 2001). In the early 1980s, Shanxi province imported large quantities of unprocessed ponderosa pine logs for coal mine braces per year, which is one of *D. valens*' hosts in western US. *D. valens* can be speculated experienced a repeated introduction of individuals in its early arrival. This repeated introduction provided successive colonists for a new habitat and increased the possibility of the invasion. More recently studies of DAN series of *D. valens* both in the United States and in China proved that Chinese *D. valens* came from multiple sources in the United States (personal communication with Anthony Congeto, Texas A & M University). This multiple introduction made the invasive populations more genetically diverse, and different colonizing populations of this species with different levels of genetic variation have different capacities to promote invasiveness. There must be one or more genetically different populations that were fit for the new environment stress and evolved to be established populations. *D. valens*, wide range in North America suggests this beetle is of high phenotypic plasticity and relatively easy to adapt to different environmental stresses, and thus the high phenotypic plasticity explained in part its successful colonization in China.

Species that are more likely to establish a viable self-sustaining population have some traits characteristics: higher intrinsic rates, r-selected strategy (smaller body sizes, use of pioneer habitat, short, generation time, high fecundity, high growth rates) (Crawley 1986), and thus higher rates of population growth and higher carrying capacity (Lawton and Brown 1986). These species should also have superior ability to exploiting local resources when compared with native residents (Sakai et al. 2001). The traits characteristics of *D. valens* such as higher fecundity, short generation time, r-selected strategy, high phenotypic plasticity, and very high dispersal capability can be used to explain the beetle's successful colonization and establishment. Within communities as recipient, lack of competitors, lack of effective predators and pathogens, abundance of resources, and the phylogeographical structure that facilitate the beetle's dispersal are all favor the beetle's successful establishment and subsequent spread. The circumstances *D. valens* encountered in China were mostly accorded with the susceptibility of communities. Table 4 is a

Table 4. Traits of *D. valens* that favor its colonization, establish, and spread in China.

Relative size of insect body	Medium in the regression curve of species body vs probability of invasion, indicating *D. valens*' possible invasion
Mating system and Fecundity	Sexual production; Sibling mating increases mating opportunities; large number of progeny per female (up to more than a hundred). All of these provide a large number of heirs for colonization and sequent dispersal
Crypsis	High level of crypsis (boring under barks and body's color similar to that of bark) except dispersal reduces the possibility of the beetles being predated by natural enemies or being detected by scrutators
Number of generations per year	1–3 generations per year and overlapped generations also assures the continuous colonization and dispersals
Phenotypic plasticity	High. Wide range of habitats in North America indicates *D. valens* has ability to adapt to environmental variations and stresses, this favors the beetle's colonization and establishment in China
R-selected vs K-selected strategy	Tending to r-selected strategy (use of pioneer habit, short generation time, high fecundity, and high growth rate) also affords the beetle sustaining a large population size.
Dispersal capability	Very high. Flight distance is at least 60 cm and 15 km at most per time (Wang et al. 2002); The farmost flight distance is 35 km. Considering that the distances between adjacent stands seldom exceed this distance, *D. valens*' dispersal is unblocked.

comprehensive conclusion of the factors contributing to *D. valens*' successful establishment and rapid spread.

Potential evolutionary

Invasive species may evolve both during their initial establishment and subsequent range expansion, especially in response to selection pressures generated by the novel environment. Hybridization, either interspecific or between previously isolated populations of the same species, may be one important stimulus for the evolution for the evolution of invasiveness; inbreeding may be another important stimulus (summarized by Sakai et al. 2001).

In general, genetic drift during colonization may bring about reduced genetic variation in newly established population because small number of initial colonists in the isolated small self-producing population. Inbreeding depression may limit population growth and the probability that the population will persist (Sakai et al. 2001). But the multiple introduction of *D. valens* can create much more genetically diverse populations than any single source because of the genetic variation of *D. valens* populations in its original sources. This, in part, counteracts the disadvantage of the genetic drift. From the introduction to the detection, *D. valens* was expected to have experienced a lag time. Lag times are expected if evolutionary change is an important part of the colonization process, including the evolution of adaptation to the new habitat, the evolution of invasive life-history characteristics, or the purging of genetic load responsible for inbreeding depression (Sakai et al. 2001). The lag time of *D. valens* could be a result of the time required for adaptive evolution to overcome these genetic constraints.

Dendroctonus valens has a strong flight capability, it spread rapidly from Shanxi province to three other adjacent provinces (Hebei, Henan, and Shaanxi). Highly dispersal rates are expected to bring about a large amount of gene flow. Whereas high gene flow would help to bring genetic diversity to the edge of the range of a species, although they may also act to constrain adaptation to local conditions (summarized by Sakai et al. 2001). In spread process, *D. valens* was expected to have evolved in one after another new ranges.

This evolutionary process may result in different populations fit to different habitats in different environments. But these are only a speculation, future studies need to be conducted.

Favorable climate

Suitable climate and hosts have undoubtedly contributed to *D. valens*, establishment and spread in northern China. First, increase of humidity, especially consecutive rainfall disrupts the growth of larvae and eggs of *D. valens* (Miao et al. 2001), however, precipitation in northern China is generally lower than in other regions of China, especially from October to May (Sun et al. 2002). Wu and Feng (1994) divided *P. tabuliformis* forest into four climatic regions (Table 5). Northern China's *D. valens* outbreak occurs within the warm temperature semi-moist region, which has precipitation that is one half to one third that of the other regions; relative humidity is the lowest of the four climatic regions and mean length of sunlight per year is the longest. Also evidence suggests northern China has become drier (Sun Shuqing et al. 2002). Several recent consecutive years of drought have stressed *D. valens*' primary host, *P. tabuliformis* and contributed to the current outbreak (Li et al. 2001). Second, higher than normal temperatures during the past 4 years in Shanxi Province have also favored favors *D. valens* survival (Miao et al. 2001). Winter temperatures, in particular, have been warmer than in previous years and appear to be critical in beetle survival (Xu et al. 1986; Li et al. 2001). Many years separate the first known introduction of RTB in China in the early 1980s and its first outbreak in 1999 (Li et al. 2001). Recent changes in climatic conditions appear to favor the beetle and may be partially responsible for this time lag.

Table 5. Climatic factors of *P. tabuliformis* forest[a] (Cited from Wu and Feng 1994).

Climatic region	MAAT[b] (°C)	MAP[c] (mm)	MLL[d] (hour)	≥5 °CAT[e] (°C)	ARH[f] (%)	FDY[g] (day)
Warm temperature semi-moist region[h]	6.8	361	2923	3425	49	149
Warm temperature wet-semi-moist region	12.2	689	2098	4315	66	199
Warm temperature moist region	5.2	899	2372	3341	69	138
Subtropical moist region	17.9	1038	1569	5139	78	266

[a] Based the data collected from 1980 to 1989.

[b] Mean annual air temperature.

[c] Mean annual precipitation.

[d] Mean length of sunlight, the average sum of sunshine hours per year in a period.

[e] ≥ 5 °C year accumulative temperature, the total sum of mean day temperatures above 5 °C in a year.

[f] Average relative humidity.

[g] Frost-free days per year.

[h] The RTB outbreak falls within the 'warm temperature semi-moist region', precipitation in this region is one half to one third of that of the other regions, and relative humidity is the lowest of the four climatic regions.

Distinct behavioral characteristics of chinese D. valens

Because roots provide greater protection from the cold, it is possible that selective pressures have favored *D. valens* that reproduce in roots over those that reproduce in the lower stem. Overwintering in roots reduces beetle mortality in winter (Miao et al. 2001) and *D. valens* cannot overwinter in boles when the temperature is under −18 °C (Wu et al. 2002). In recent years, the lowest temperatures have seldom been dropped below this point (Unpublished data from Shanxi Provincial Meterological Bureau), which should have expanded suitable overwintering sites and beetle survival. This may keep relatively large number of individuals to continue the establishment or the dispersal to adjacent regions. In addition, *D. valens* lives under the barks of logs or timbers and the beetle's color is similar to the bark's color. These crypsises reduce the probabilities being detected and predated by its predators and enhance the probability being transported unconsciously by human activities.

The number of eggs a female *D. valens* lays is from a few to more than a hundred. The number of generations per year is 1 (in cold regions) to 3 (in warmer regions) (Smith 1961, Vité et al. 1964; Zhang et al. 2002). This high fecundity, rapid growth from seedling to sexually maturity (short generation time), and r-selected strategy resulted in higher rates of population growth and higher carrying capacity, and thus favored the establishment and the sequent dispersal.

Both in the United States and in China, *D. valens* is very capable of extended flight. It was reported that the flight distance is at least 16 km in the west United States (Smith 1970), or up to 35 km in China (Zhang et al. 2002). This strong flight potential affords the beetle to move from the initial stands to a new habitat, even though the two regions are blocked by unforested areas. In fact, there is seldom two stands the distance between them is exceeds 35 km in *D. valens*-infesting areas in China, because the pine forests distribute along with the cordillera of the Luliang mountains and the Taihang mountains, and from mainly two belts. In the view of these points, the spread of this beetle is resistless.

Characters of host pine species in China

Human activities including logging and farming have significantly degraded *P. tabuliformis* stands in many parts of China, resulting in a lower diversity of tree understory plant and insect groups. A 5-year investigation of degraded *P. tabulaeformis* stands in northern mountainous areas of Hebei Province in China (Gao et al. 1999) illustrates this situation. In selected stands, the numbers of plant and Insect families were reduced by 55 and 60%, respectively; species and family-species diversity indices of plant communities were reduced by 22 and 29%, respectively; and species and family-species diversity indices of insect communities were reduced by 38 and 47%, respectively. In stands that experienced a 19-year protection period, numbers of insect species and families were more than those of unprotected stands by 52, 82%, respectively, species and family-species diversity indices of insect community in the protected stands were more than those of insect community of unprotected stands by 114, 56%, respectively (Gao et al. 1999). Stands that have experienced logging or thinning are preferred by *D. valens* (Furniss and Carolin 1977; Miao et al. 2001). This may be due in part to the creation of fresh stumps that provide breeding sites for *D. valens*. These activities may also have a negative impact on natural enemies and competitors of RTB.

P. tabuliformis, is one of the most widely distributed pines in China. It grows over a vast area in northern and north-central China, from 31°N to 44°N latitude and 101°30′E to 124° 25′E longitude (Wu and Feng 1994). This abundant distribution *of P. tabuliformis* (and *P. armandi* and *P. bungeana*) provides abundant habitats for *D. valens* beetles. Seven ecotypes (Figure 3) are recognized *D. valens*-infested areas in central and southern Shanxi province, western Hebei, and northeastern Henan belong to the 'middle' ecotype, and the infested part of Shaanxi belongs to the 'middlewest' ecotype. The middlewest and south ecotypes of *P. tabuliformis* may suffer cold-related damage in middlewest and south ecotypes (northern Shaanxi and Henan provinces) (Xu et al. 1986) Such damage may make *P. tabuliformis* vulnerable to *D. valens* attack in the spring. Most *P. tabulaeformis* stands in these areas are monocultures, thus providing a concentrated food source for *D. valens*. Consequently, northern Shaanxi provinces should be viewed as possible sites for future as *D. valens* outbreak.

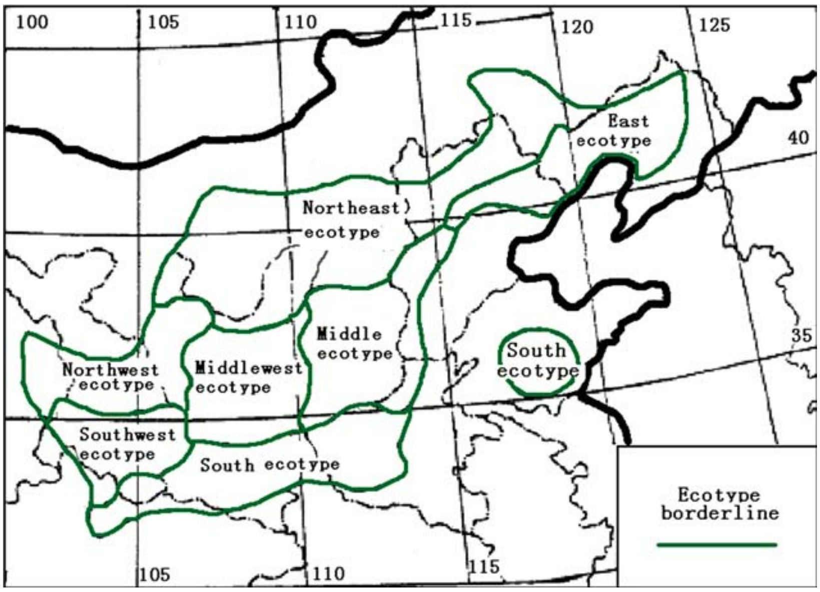

Figure 3. Distribution *P. tabuliformis* ecotypes in China (from Xu et al. 1986). The current *D. valens* distribution occurs almost entirely in the Middle ecotype, the southeast part of the South ecotype and the southern part of the Middlewest ecotype. Cold-related damage in the middlewest and south ecotypes (north of Shaanxi and Henan province) may make *P. tabuliformis* vulnerable to *D. valens* attack in the next spring.

Meltdown-synergistic invasion

In the western US, *D. valens* vectors *L. terebrantis L. procerum*, *C. ips*. These fungi can infest the pine hosts and weaken their livingness (Owen et al. 1987; Klepzig et al. 1991), whereas weakened hosts are vulnerable to attack by *D. valens* (Smith 1971). It may be speculated that *D. valens* and the associated fungi are symbiotic; *D. valens* beetles vector the associated fungi to pine hosts which also are suitable trophic resource for the fungi, and the fungi make the hosts more susceptible to other *D. valens* beetles. In China, dead *P. tabuliformis* killed by *D. valens* boring activities were found to be infested by some fungi/fungus, and some fungi have been isolated from adult *D. valens*. If the case in China is consistent with that in the west US, it may be said that *D. valens*' invasion and the later spread are symbiotic with its associated fungi.

Lack of native competitors

In the *D. valens*-infesting areas, the congeneric species are *Dendroctonus micans* Kugelann and *Dendroctonus armandi* Tsai et Li. The two congeners are of lower densities and have not caused significant impacts on their hosts. Lack of native competitors, combined with wide distribution of host pines, offers large numbers of empty niches for *D. valens* invasion and spread.

Lack of natural enemies

In North America, *Rhizophagus grandis*, *Enocleris lecontei*, *Thanasimus undatulus*, *Thanasimus dubius*, *Platysoma cylindrica*, and *Tenebroides collaris* (Hall 1983; Paine and Hanlon 1991; Krokene and Solheim 1998; Erbilgin and Raffa 2000) are predators of *Dendroctonus* spp. The role of such predators in regulating *D. valens* populations is unknown. None of these predators are believed to be present in China. Some *D. valens* predators, parasites and fungal diseases have been found in *D. valens*-infested areas in northern China (Zhang et al. 2002; Wu et al. 2002), but their impact on *D. valens* populations is unknown. A Tenebrionidae species reared in the laboratory killed *D. valens* adults and the fungi *Beauveria Vuill*; and *Metarrhizium anisopliae* killed larvae, adults, and pupae of *D. valens* (Wu et al. 2002). Among seven species of nematodes tested, *Steinernema ceratophorum*, a nematode isolated from Jilin province in northeast China, produced the highest infection rate of mature *D. valens* larvae, causing 90% mortality of the larvae after a 96-h exposure. However, this nematode has not been found in *D. valens*-infested areas and its practical use needs investigation (Jian et al. 2002).

The rapid expansion of *D. valens* populations in recent years could mean that natural enemy populations are yet lagging behind and their impact has not yet been fully realized.

Impacts on native chinese biodiversity

Significant genetic and evolutionary changes in both the native and invasive species may occur. Both genetic drift and natural selection (from biotic interactions and abiotic factors in the new environment) may cause rapid evolution in the invasive species. As a consequence, rapid evolutionary changes also may occur in the native species. In the extreme, hybridization and introgression between invasive and native species may result in extinction of the native species (summarized by Sakai et al. 2001).

Dendroctonus valens has not aroused any attention before being detected in 1998 (Miao et al. 2001). It has finished its colonization and establishment stages, and become a permanent inhabitant in its new habitats in China. Thus, impacts on native biodiversity is a long-term, and can forever change important forest ecosystem process thereby affect uses of forest resources for timber, recreation, wildlife, etc. Its interactions with native insects infesting pine (include the two congeners *D. Kugelann* and *D. armandi)* and native disease organisms are unknown. How the beetle interacts with other pine-feeding insects or alters their interaction with host pine will, in part, determine long-term impacts. The interaction with other organisms within the pine pest native range will be useful for the study in China. All of these remain to be studied.

Since its first outbreak in 1999, *D. valens* has cause severe mortality and decline of livingness of *P. tabuliformis* stands. If the mortality and decline continues, some of these stands may be greatly or completely eliminated, possibly resulting in extinction of native species that are tightly associated with pine species.

Pine species, including *P. tabuliformis*, has been widely planted in high elevation areas for several decades in the northern China, because of the pine species cold-resistance and drought-resistance. These pines (*P. tabuliformis*) play significant roles in water and soil conservation in the fragile ecosystem of barren mountainous areas. Mortality or decline of pine forests caused by *D. valens* will aggravate soil erosion, resulting in adverse circumstances for other native faunas and floras and thus reduction or change of plant species and animal species. Regulation function of forests on conditions is unquestionable. Continuation of the damage of the pine forests may cause some climatic changes; thereby cause the changes of ecological populations.

D. valens management

Prior to 1999, *D. valens* was not considered a forest pest in China. However, its pest status is steadily increasing as the beetle continues to spread and cause damage. The Chinese State Forestry Administration currently ranks it as the second most important national forest pest. A National Management Project was initiated for *D. valens* in 2000. In 2001, eastern Shaanxi became infested; about 30% of the 85,300 ha of pine forest in the province have been infested, with about 7% mortality of *P. tabuliformis* in 2001. In 2002, *D. valens* infestations extended into Henan province, but quick action by the State Forestry Administration appears to have kept damage to a minimum.

Monitoring and prevention

Monitoring is an important tool for slowing and preventing the spread of *D. valens*. Artificial spread by humans appears to be the principle means of spread in areas where pine stands are widely separated. Any pine material with intact bark could potentially harbor *D. valens*. Harvesting of green trees creates breeding habitat for *D. valens* in stumps, potentially aggravating or initiating outbreaks, while harvesting of dying, infested trees may facilitate *D. valens* spread through movement of infested logs. Restrictions on unauthorized tree harvesting and the movement of infested material (logs, wood blocks, and wood boxes with bark) have been strictly enforced. Strict quarantine regulations have been issued and enforced at ports, along highways and railways within infested areas. No timbers that may harbor *D. valens* can be transported out of infested areas without permission.

Long-term solutions need to address stand and tree susceptibility to *D. valens*. To a certain extent, historical records and protected natural areas can serve as models for stand rehabilitation, with the understanding that *D. valens* must now be taken into consideration as a significant ecological factor. *D. valens* is likely to be a driving force behind the management of affected forests for many years to come. A better understanding of the interaction between *D. valens* and forest stand attributes will enable managers to devise silvicultural treatments that result in stands that are more resistant to beetle attack. It will be important to consider other forest insect pests and tree diseases in designing treatments. Not only can these other pests affect tree susceptibility to *D. valens*, but achievement of future desired stand conditions will depend upon the forest's response to all potential pests and treatments.

Surveillance of the occurrence of this pest and prevention from its spread may be long-range tasks. The *D. valens* investigation has been monitored annually since 1999. Plots are inspected in the summer and the fall for indicators of the attack, such as pitch tubes and boring material. A plot with one or more attacked trees is recorded as *D. valens* infested. Based on data offered by the Shanxi Forestry Bureau, the *D. valens*-infested area within the province has decreased from 255,720 ha in 1999 to 178,000 ha in 2002 in Shanxi, province (Figure 4). A number of factors may have contributed to this climatic conditions less favorable to *D. valens*, prohibition of unauthorized tree harvesting and movement of *D. valens*-infested materials, and direct control of beetle populations.

Control

Fumigation of boles with aluminium phosphide under plastic cover, dimethyl dichloroviny phosphate (DVVP) or Omethoate injection into newly initiated galleries, and spraying insecticides (Phorate, Monocrotophos, Cypermethrin, and Phoxime, etc.) onto boles during the flight period are direct control methods that all have been shown to be effective at killing beetles by 90–98% mortality (unpublished data from Shanxi Forestry Bureau). Manual control, such as felling and digging out the stumps of dying or recently dead pine trees and eliminating exposed roots and stumps, may also be used to eliminate beetles. Trapping beetles using semiochemicals lures (host volatiles) is a laborsaving, environmental friendly and promising method. Both male and female beetles are trapped and the method can be used in all seasons that the beetle is active. When a 1:1:1 blend, of (+)-α-pinene. (−)-β-pinene, and 3-carene was used in an operational mass trapping program, from 10 May to 23 June, on the Guandi Mountain, west of Shanxi province, the proportion of infested forest decreased by 64.4% and the average number of attacks per tree decreased by 59.2% (Guo et al. 2003). Flight of overwintered *D. valens* adults

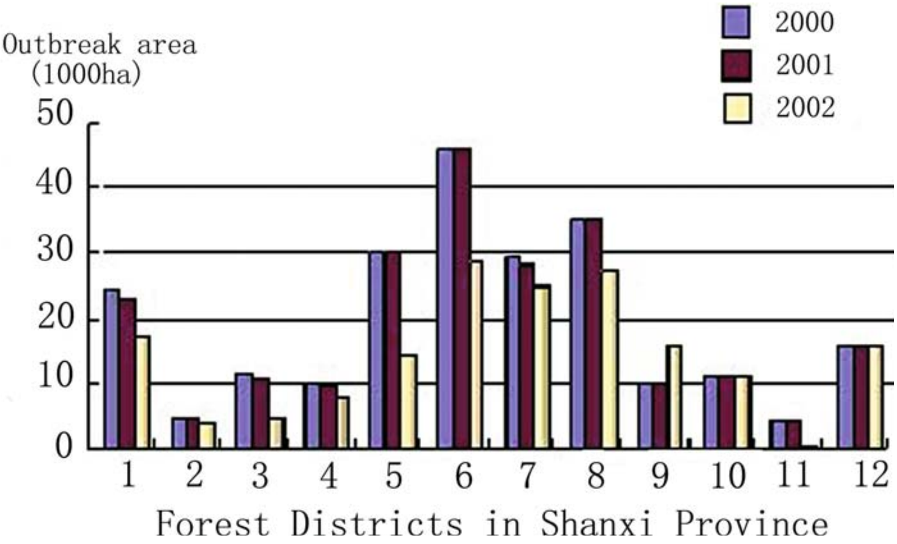

Figure 4. Area (1000 ha) of *D. valens* infestation in twelve districts of Shanxi (unpublished data Shanxi Forestry Bureau). 1 – Linfeng, 2 – Yangquan, 3 – Taiyuan, 4 – Luliang, 5 – Changzhi, 6 – Jinzhong, 7 – Jincheng, 8 – Zhongtiao Mountain, 9 – Guandi Mountain, 10 – Taiyue Mountain, 11 – Luliang Mountain, 12 – Taihangshan Mountain.

begins in mid April and peaks in mid May. During other months of a year, numbers of trapped adults are less. Pupation of overwintered larva begins in early June, and eclosion begins in early July (Miao et al. 2001). Thus, from mid April to early June is the best time to mass-trap flight beetles. Fumigation and injection with insecticides can be used all over the year, but the optimal time is early June to October during which pupation of overwintered larva and development of new larvae occurs.

Application of these control techniques is believed to have impacted the *D. valens* population. According to data from the Shanxi Forestry Bureau, the *D. valens*-infested area decreased from 255,720 ha in 1999 to 178,000 ha in 2002 in Shanxi province (Figure 4).

However, chemical control (fumigation) is costly and difficult to apply, and has never been proven effective at controlling beetle populations over large areas. It can also result in environmental contamination and decrease in natural enemy populations. Manual control is labor intensive and not deemed practical.

Although the use of semiochemicals to manipulate beetle populations holds promise as a management tool well controlled studies are needed to demonstrate effectiveness, with the ultimate goal being a reduction in tree mortality. The potential gains from semiochemical treatments would likely be short-lived if environmental conditions remained unchanged. Their use would be appropriate in combination with long-term solutions, such as silvicultural treatments or in situations where tree susceptibility or high beetle populations are expected to be of limited duration, such as during periods of temporary drought or in conjunction with tree harvesting operations that allow beetle populations to increase by breeding in fresh stumps.

It is unknown to what degree natural enemies regulate *D. valens* populations in China and in its native range. Strategies for augmenting *D. valens*, natural enemies include: cultivation of local natural enemies, introduction of natural enemies from the beetle's native range, and introduction of natural enemies of similar or related beetle species. Introduction of exotic natural enemies into China needs to be done with adequate safeguards to prevent unwanted impacts to native fauna and flora. Negative impacts potentially could result directly from candidate natural enemies or from associated organisms. Sub-cortical insects are known vectors of a wide range of organisms – fungi, mites, nematodes, bacteria, etc. that could accidentally be introduced with unknown consequences (Owen 2001). On the positive side, the introduction and establishment of exotic natural enemies potentially could provide long-term regulation of *D. valens* populations and reduce the need for other treatments.

While *D. valens* is widely distributed in North America, populations in different sites have different behavior and different gene series (described as above). These indicate that there may be behaviorally and genetically different populations in China. Studying these differences will promise more effective controlling methods depend upon different behaviors. For example, different host volatiles [(+)-α-pinene or (−)-β-pinene] can be used in different sites.

Research recommendations

Genetics and variation

In its extensive native range, *D. valens* populations exist in a variety of habitats with many different primary hosts. Variation in *D. valens* populations throughout this range is poorly understood, as are variations of associated microorganisms that may have been introduced to China concurrent with *D. valens*. Differences between the behavior of *D. valens* in China and that of its original conspecific groups are likely an indication of this variation, but may also reflect adaptation to a new environment. Comparative studies of *D. valens* biology in China and the Americas will help answer many basic and applied questions about bark beetle biology, in addition to providing a better understanding of the potential spread and impact of *D. valens* . Environmental impact and biosecurity are important issues especially considering the broad geographic/host range of *D. valens* and the diversity and continuity of *Pinus* spp. across Eurasia.

To what degree have *D. valens* populations in China evolved since the beetle's introduction? Has *D. valens* undergone any changes in physiology or behavior? What *D. valens*-associated fungi are present and where did they come from? Are they introduced or are they acquired native species? What is the impact of these fungi on Chinese *Pinus* spp.? Is there variability among individual trees and between tree species in the way they respond to fungal inoculation? Does this variability correlate with *D. valens* success? How do fungal inoculations on roots compare to those on the main stem? All these questions need to be studied and answered.

Chemical communication

To date, semiochemicals known to influence *D. valens* behavior are volatiles of host trees and pheromones of other bark beetle species. No pheromone has been identified for *D. valens*. There are a number of activities critical to the success of bark beetle populations that may be mediated by chemical and other forms of communication: (1) attracting a mate, (2) colonizing and exploiting a host, (3) minimizing intra- and interspecific competition, and (4) avoiding natural enemies. Each attempt to attract attention to itself increases a beetle's likelihood of experiencing both the benefits and costs of chemical communication. Individual success depends on the extent to which a beetle can maximize the former and minimize the latter.

The differences in response of RTB to host volatiles in China versus the Western United States indicates there is a great deal to learn about the beetle's chemical ecology. Documenting variations in beetle response across its extensive native range should provide insight to the origin of RTB in China. Does the beetle's response to host volatiles in China correspond with a unique or varied group of conspecifics in North America? Or perhaps new behavioral traits have emerged in China. Might the beetle's origin be influencing its choice of hosts in China? How might response change as the beetle encounters new hosts? Several joint studies are under the way both in China and North America in an attempt to address many of the above questions.

The potential spread of D. valens *in China*

The distribution of *Pinus tabuliformis* overlaps that of *P. armandi*, *P. bungeana* and borders on *P. massoniana* (Figure 2). Although the distribution of pine forest stands in China is separated by expansive croplands and unforested areas, *D. valens*' spread has been fairly consistent in Shanxi. However, *D. valens* has not yet been found in two northern districts of Shanxi where *P. tabuliformis* is abundant but the winter temperatures are low. During 1997–2001, there were more than eight days each January in these districts when temperature were below −20 °C (unpublished data from Shanxi Provincial Meterological Bureau). The low temperature may partially account for the obsence of *D. valens*. The oleoresin compositions of *P. massoniana* and *P. armandi* are similar to that of *P. tabuliformis*

(Table 3), so *P. massoniana* and *P. armandi* are presumed to be susceptible to *D. valens* infestation. Thus far, *D. valens* attacks have been found on all pine species that the beetle has encountered in China. The beetle's wide host range in North America would suggest that all Chinese pine species will be attacked and its spread will continue to other areas where climate conditions fit its survival. Still, the spread of *D. valens* to other parts of China, and possibly beyond, will not easily be predicted due to a complex of factors that define host and environmental suitability. However, does *D. valens* prefer *P. tabuliformis* to its other sympatric pine species? Or does it only infest *P. tabuliformis* severely, whereas *P. armand*, and *P. bungeana* are, in some respects, unsuitable to its infestation? All these questions await further study. If the difference of infection frequencies between *P. tabuliformis* and the sympatric pine species consists in difference of their genotype, reforestation efforts could potentially benefit from the use of resistant genotypes and resistant species mixes.

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